

## Intrapopulation Body Size Variation and Cranial Capacity Variation in Middle Pleistocene Humans: The Sima de los Huesos Sample (Sierra de Atapuerca, Spain)

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**ABSTRACT** A sexual dimorphism more marked than in living humans has been claimed for European Middle Pleistocene humans, Neandertals and prehistoric modern humans. In this paper, body size and cranial capacity variation are studied in the Sima de los Huesos Middle Pleistocene sample. This is the largest sample of non-modern humans found to date from one single site, and with all skeletal elements represented. Since the techniques available to estimate the degree of sexual dimorphism in small palaeontological samples are all unsatisfactory, we have used the bootstrapping method to assess the magnitude of the variation in the Sima de los Huesos sample compared to modern human intrapopulation variation. We analyze size variation without attempting to sex the specimens *a priori*. Anatomical regions investigated are scapular glenoid fossa; acetabulum; humeral proximal and distal epiphyses; ulnar proximal epiphysis; radial neck; proximal femur; humeral, femoral, ulnar and tibial shaft; lumbosacral joint; patella; calcaneum; and talar trochlea. In the Sima de los Huesos sample only the humeral midshaft perimeter shows an unusual high variation (only when it is expressed by the maximum ratio, not by the coefficient of variation). In spite of that the cranial capacity range at Sima de los Huesos almost spans the rest of the European and African Middle Pleistocene range. The maximum ratio is in the central part of the distribution of modern human samples. Thus, the hypothesis of a greater sexual dimorphism in Middle Pleistocene populations than in modern populations is not supported by either cranial or postcranial evidence from Sima de los Huesos. *Am J Phys Anthropol* 106:19–33, 1998. © 1998 Wiley-Liss, Inc.

The absence of knowledge of the range of size variation within fossil species is a major problem in palaeontology, and affects the ability to recognize different species. Often this critical issue can only be tackled using actualistic criteria, that is, basing the estimate of variation on closely related extant species whose ranges of variation are used as yardsticks with fossil samples.

Sexual dimorphism is a potentially major source of size variation within a population

(Wood, 1976). Unfortunately, among the closest living relatives of fossil hominids, there are very different degrees of sexual dimor-

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phism (and thus intraspecific variation) in size, as observed in living humans, chimpanzees and gorillas. In fact, sexual dimorphism is a species-specific characteristic (or better a population-specific characteristic), and can vary among species (and to a lesser extent among populations) not only in degree but also depending on which part of the body is analyzed (i.e., in pattern). For instance, sexual dimorphism in body size in hominid species varies from similar to much greater than in chimps, but all hominids are clearly less dimorphic in canine size. Further, sexual dimorphism has a genetic component and an environmental component, and in modern humans it is known that the degree of sexual dimorphism is influenced by stress (nutritional, epidemiological, etc.), by labour division and by social roles (Borgognini-Tarli and Repetto, 1986; Frayer, 1980).

Very often human fossil samples consist of specimens spanning large chronologic and geographic ranges, and thus geographic differentiation and phyletic evolution are also potential sources of variation. Henneberg (1990) found that in brain size and body weight about half of the intraspecific variance in modern humans results from differences between individuals of the same sex within a population (intrasexual variation), the between-populations component contributes slightly less than 30% to the species total, and sexual dimorphism contributes less than one-quarter of the total variance. On the other hand, according to Henneberg (1992), in the last 10,000 years cranial capacity underwent a decrease by more than 10%, and stature fluctuated. Thus working at the population level in human palaeontology eliminates two important sources of variation: interpopulational variation and variation due to phyletic evolution.

In the Sima de los Huesos (SH) in Sierra de Atapuerca (Spain) there is a large human sample that comes from a single contemporary (or almost contemporary) Middle Pleistocene population, and provides a unique opportunity to investigate within-populational variability. The variation established can be compared with that of modern human populations.

The minimum number of individuals in SH has been estimated at 32 based on the

dental sample (Bermúdez de Castro and Nicolás, 1997). The fossils have been directly dated by U-series and ESR to more than 200,000 years ago with a probable age of 300,000 years ago (Bischoff et al., 1997). These dates are compatible with the faunal content of the site in terms of large mammals (García et al., 1997) or small mammals (Cuenca et al., 1997). The Sima de los Huesos sample corresponds to a population ancestral to Neandertals, exhibiting a mosaic of primitive traits, combined with some (in general incipient) Neandertal derived traits (Arsuaga et al., 1991, 1993, 1995b, 1997b; Carretero, 1994; Carretero et al., 1997; Martínez and Arsuaga, 1997). All skeletal elements are represented in the human collection in large numbers; in fact, the SH postcranial sample represents more than three-quarters of the human fossil record for the whole Middle Pleistocene, and the collection will certainly expand substantially in the coming years. There are individuals of different ages, with a predominance of adolescents and prime-age adults, and few infants and older adults.

Although many methods have been designed to evaluate the degree of sexual dimorphism (Borgognini-Tarli and Repetto, 1986), unfortunately they are calculated on individuals of known sex or skeletally diagnosed sex.

To Wolpoff (1980), the European Middle Pleistocene crania show more sexual dimorphism than modern humans, although not significantly more than the Neandertals. Steinheim and Petralona were the most extreme values within the European Middle Pleistocene sample. Based on samples of skeletons sexed on the morphology of the pubic symphysis, when available, or on the cranial morphology, Frayer (1980) concluded that dental, cranial and body size dimorphism experienced a substantial decrease from the Upper Palaeolithic to Neolithic. To Frayer, the major cause for this decrease is gracilization of the males, which in turn is tied to a shift in male activities: in the Upper Palaeolithic males were engaged in the hunt at close-quarters of large preys. According to this point of view the study of sexual dimorphism in human fossil samples also informs us about the degree of division of labour by

sex. Frayer and Wolpoff (1985) considered that Middle and Upper Pleistocene hominids display levels of dimorphism intermediate between *Australopithecus* and extant groups.

In contrast, Trinkaus (1980) concluded that sexual dimorphism in limb bone size and robusticity in Neandertals was virtually the same as that of recent human samples, but this author also first sexed the specimens based on pelvic morphology when possible or otherwise based on absolute size. This is a serious methodological drawback, because of the circularity involved in determining sexual dimorphism on the same feature (size) that is used for sex diagnosis: the approach presupposes sexual dimorphism in order to estimate it. In the same way, Oleksiak (1986) concluded that Neandertals and early modern human present the same degree of sexual dimorphism. It is better to apply methods that do not require prior sex estimation of the fossils.

Lovejoy et al. (1989) developed a new method to estimate the degree of sexual dimorphism in skeletal samples of unknown sex that they applied to *Australopithecus afarensis*, under the assumptions that the sample to be analyzed contains at least one member of each sex and that any male in the sample is larger than any female in the sample. They claimed that their technique was tested in over 2,300 simulated samples derived from real primate data, finding that error is relatively small for moderate to large values of skeletal dimorphism (1.10 or greater) and the sample size excess of 14 individuals. On the other hand, Plavcan (1994) showed that when the levels of dimorphism are low (from 1 to roughly 1.3), the degree of sexual dimorphism cannot be reliably estimated from pooled-sex samples using coefficients of variation, division of a sample in two subsamples about the mean or median, and finite mixture analysis. To Plavcan (1994), since these methods rely on the assumption that as the means of the two underlying male and female distributions get further apart in the population, the variation of the pooled-sex samples tends to increase, they are potentially confounded by fluctuations in sex ratio, small sample sizes, and fluctuations in intrasexual variation. We would add that in fossil samples covering

large geographic and chronologic ranges, interpopulational variation, directional trends or diachronic fluctuations can contribute more to the sample variation (even if the sample is large) than sexual dimorphism (this would not be the case of the Sima de los Huesos sample if, as we believe, it comes from one single population). Josephson et al. (1996) used the method-of-moments to estimate the degree of sexual dimorphism in samples of unknown sex. It has the advantage over other methods of allowing estimation of confidence intervals. Since the procedure uses three moments around the mean of the combined-sex distribution to estimate the means and the standard deviations of the male and female distributions, the required sample size is usually far beyond the availability of the fossil record of ancient hominids.

Some authors simply do not attempt to measure directly the degree of sexual dimorphism of a fossil sample and they concentrate instead on the likelihood of obtaining by chance a fossil sample with a given variation. In this sense this is a hypothesis test, and the null hypothesis is that the sample comprises an analog of the variation in a living species. If none or very few samples randomly generated from the extant species show a level of variation greater than that of the fossil sample, the null hypothesis (i.e., the level variation of the fossil species is the same or lesser than that of the extant species) is rejected. In the opposite case, the null hypothesis is not rejected (that statistically is not the same as being confirmed).

For example, in a previous work using a specially designed statistical procedure to deal with small size samples and non-sexed specimens, Bermúdez de Castro et al. (1993) concluded that sexual dimorphism in teeth (only lower dentition was analyzed) was more marked in the Sima de los Huesos sample than in modern humans. Lieberman et al. (1988) randomly sampled 20 pairs of male and female gorillas to determine the distribution of the male/female ratio for various traits, in order to estimate the probability of sampling a male individual and a female individual as different as KNM-ER 1470 and KNM-ER 1813. Grine et al. (1993)

TABLE 1. Variables used in this analysis

Cranium:	Cranial capacity (cm <sup>3</sup> ) using the seed or water method.
Scapula:	Glenoid fossa height (M#12); Glenoid fossa breadth (M#13).
Humerus:	Proximal epiphysis breadth (M#3); Vertical diameter of the humeral head (Carretero et al., 1997); Transverse diameter of the humeral head (M#10); Biepicondylar breadth (M#4); Midshaft perimeter (M#7a).
Ulna:	Olecranon breadth (medio-lateral diameter) (M#6); Olecranon height (anterior-posterior diameter) (McHenry et al., 1976); Coronoid breadth (medio-lateral diameter) (M#6.1); Coronoid height (anterior-posterior diameter) (McHenry et al., 1976); Trochlear anterior-posterior diameter (McHenry et al., 1976); Proximal perimeter: perimeter of the shaft taken at the position along the shaft at the level of the distal border of the tuberosity; Midshaft perimeter.
Radius:	Neck perimeter (M#5.4).
Coxal:	Vertical acetabular diameter (Arsuaga and Carretero, 1994).
Sacrum:	Transverse diameter (width) of the first sacral vertebra (M#19); Anterior-posterior diameter (height) of the first sacral vertebra (M#18).
Femur:	Vertical diameter of the head (M#18); Medio-lateral diameter at the subtrochanteric level (just below the lesser trochanter) (M#9); Anterior-posterior diameter at the subtrochanteric level (just below the lesser trochanter) (M#10).
Patella:	Maximum height (M#1); Maximum breadth (M#2); Patellar thickness (M#3).
Tibia:	Midshaft perimeter (M#10).
Talus:	Trochlear length (M#4); Trochlear breadth (M#5).
Calcaneus:	Maximum length (M#1.1); Body length (M#5); Sustentaculum tali breadth (M#6); Body height (Steele, 1976)

M# refers to measurements in Martin and Saller (1957).

employed an exact randomization procedure to assess the magnitude of distances between the partial *Homo* cranium SK 847 and crania KNM-ER 3733 and KNM-WT 15000, which had been attributed to the same species. Richmond and Jungers (1995) also used the exact randomization method to compute all possible pairwise ratios of metrical variables in samples of extant species of hominoids and compared them to the maximum ratio of the sample of *Australopithecus afarensis*. Since this method ignores sample size, and it is more probable to find extreme values in large samples, Lockwood et al. (1996) used the resampling method commonly referred to as bootstrapping, simulating random samples of the same size that the fossil assemblages from extant taxa.

In this paper, body size variation and cranial capacity variation are studied in the Sima de los Huesos (SH) Middle Pleistocene sample.

## MATERIALS AND METHODS

We take the approach of Lockwood et al. (1996), using the bootstrap method (Efron, 1979; Efron and Tibshirani, 1993) to compare the intrapopulation variation between the Sima de los Huesos group and modern humans, the only living species analog that is sensibly compared with a Middle Pleistocene human fossil sample. This method consists of simulating a large number of

random samples (with replacement) of the same (small) size as the fossil assemblages from extant taxa (represented by large samples). Then maximum ratios and coefficients of variations of the simulated and the fossil samples are compared to know the likelihood of obtaining by chance a sample as variable as our fossil sample (Lockwood et al., 1996).

Using only adult specimens from SH, we analyzed variables that correspond to cranial capacity; scapular glenoid fossa; acetabulum; humeral proximal and distal epiphyses; ulnar proximal epiphysis; radial neck; proximal femur; femoral shaft at subtrochanteric level; humeral, ulnar, femoral and tibial midshaft; lumbosacral joint; patella; calcaneum; and talar trochlea. Variable definitions are given in Table 1. In some cases we use the geometric mean of several variables  $[(Var_1 * Var_2 * \dots * Var_n)^{1/n}]$  as an expression of the size (Mosiman, 1970). When we suspected that two specimens of the same bone can belong to both sides of the same individual, the average of the two pieces was computed. In this study we do not use long bone lengths, thus our variables are most related, although in different degrees, to "sturdiness" (overall robusticity and muscularity, and hence weight). These aspects show sexual dimorphism in modern humans.

TABLE 2. Cranial capacity: Descriptive statistics for the Hamann-Todd pooled sex samples and Sima de los Huesos sample

	Sample	n	Mean	SD	CV	Max.	Min.	MR	ISD
Cranial capacity (cm <sup>3</sup> )	Hamann Todd Euro-Americans	184	1337	164.9	12.3	1747	1000	1.75	1.19
	Hamann Todd Afro-Americans	168	1293	125.7	9.7	1603	990	1.62	1.08
	SH	3	1245	109.6	—	1390	1125	1.24	

The Sima de los Huesos sample is composed by Cranium 4, Skull 5 and Cranium 6. Cranial capacity (in cm<sup>3</sup>) was measured using the seed method. CV = coefficient of variation; MR = maximum ratio; ISD = index of sexual dimorphism (male mean/female mean).

The modern human samples used in this paper come from the Coimbra (Portugal), Palencia (Spain) and Hamann-Todd (Cleveland, Ohio) collections of known sex skeletons. The Coimbra human skeleton collection (Coleção Esqueletos Identificados) consists of 505 skeletons kept in the Museum of Anthropology at the University of Coimbra, 498 of them coming from the Conchada cemetery of Coimbra and corresponding to individuals deceased in this city between 1904 and 1938 (Rocha, 1995). In the case of the radius we have used the raw data published by Maia Neto (1957) for the Coimbra population. The Palencia collection is kept in the Anatomical Museum at the University of Valladolid and consists of 102 individuals of known age and sex derived from the cemetery "Ntra. Sra. de los Angeles" of Palencia city. According to the historical records, all of them were people from that region of Northwestern Spain, deceased in the second half of this century. The Hamann-Todd collection is more diverse in the origin of the individuals, and derives from dissecting rooms of Cleveland hospitals. It is housed in the Cleveland Museum of Natural History. In this study we analyze separately the Euro-American and Afro-American individuals of the Hamann-Todd collection. The cranial capacity for this collection has been measured by, or under the direction of, Prof. T. Wingate Todd between 1912 and 1938, using the seed or water method (Simmons, 1942). In all the analyses of modern human samples, the proportion of males and females are equal.

In all bootstrap simulations, for each variable, we have generated 1,000 random samples, with a sample size equal to the fossil sample size. A computer program for dBaseIV was developed to generate random samples, and statistical analysis was carried out with SPSS 6.1.3 statistical package.

To metrically evaluate the level of variation we use the maximum ratio (MR = maximum value/minimum value) for all variables, and the coefficient of variation (CV = standard deviation/mean  $\times$  100) when the SH sample size is greater than five. In Tables 2 to 5 we report the comparison of the basic statistics as well as the CV and MR for the SH and modern human samples (pooling balanced sexes). The index of sexual dimorphism (ISD = male mean/female mean) is also included for the modern human samples. In Table 6 we summarize the results of the bootstrap analysis, showing the percentage of the 1,000 random samples with CVs and MRs larger than the Sima de los Huesos sample.

## RESULTS

### Cranial capacity

To Wolpoff (1980), the European Middle Pleistocene crania show more sexual dimorphism than modern humans, although not significantly more than do the Neandertals. In his study using a volumetric estimate of the brain case (made by multiplying comparable measures of vault length, breadth and height), the most extreme values within the European Middle Pleistocene sample were Steinheim and Petralona. In the Sima de los Huesos sample we found in the same excavation square (half meter on a side) an adult skull (Skull 5) with a cranial capacity of  $1,125 \text{ cm}^3 \pm 10 \text{ cm}^3$  (probably very close to that of Steinheim) and another adult (Cranium 4) with a cranial capacity of  $1,390 \text{ cm}^3 \pm 10 \text{ cm}^3$ , far exceeding that of Petralona (not much more than  $1,210 \text{ cm}^3$ ; Stringer et al., 1979). An adolescent (Cranium 6) with a cranial capacity estimated in  $1,220 \text{ cm}^3 \pm 10 \text{ cm}^3$  (after accurate reconstruction of the sphenoid bone and vault top) was also in the excavation square. Although the latter indi-



TABLE 3. Upper Limb. Descriptive statistics (mm) for Coimbra and Palencia pooled sex samples and Sima de los Huesos sample

	Sample	n	Mean	SD	CV	Max.	Min.	MR	ISD
<b>Scapula</b>									
Glenoid fossa geometric mean <sup>1</sup>	Coimbra	160	30.3	2.8	9.3	37.4	23.3	1.6	1.16
	SH	5	29.6	2.4	8.1	32.7	25.9	1.26	
<b>Humerus</b>									
Proximal epiphysis geometric mean <sup>2</sup>	Coimbra	154	42.5	3.6	8.5	52.1	32.6	1.6	1.14
	SH	4	46.2	2.6	—	48.1	41.8	1.15	
Midshaft perimeter	Coimbra	154	61.1	6.2	10.2	79	48	1.65	1.15
	SH	9	66.1	7.9	12	79	50	1.58	
Biepicondylar breadth	Coimbra	154	57.1	4.9	8.6	67.9	44.3	1.53	1.14
	SH	4	61.1	4.2	—	66	56.2	1.17	
<b>Ulna</b>									
Proximal epiphysis geometric mean <sup>3</sup>	Palencia	102	25	2.3	9.2	29.1	20.1	1.45	1.13
	SH	7	27.3	1.6	6	29.7	25.1	1.18	
Proximal perimeter	Palencia	102	51.4	6.4	12.5	68	40	1.7	1.19
	SH	9	50.6	4.4	8.8	55	41	1.34	
Midshaft perimeter	Palencia	102	45.3	5.7	12.6	60	34	1.76	1.17
	SH	7	42.5	4.4	10.3	48.3	36	1.34	
<b>Radius</b>									
Neck perimeter	Coimbra <sup>4</sup>	424	41.2	4.6	11.1	56	28	2	1.16
	SH	5	37.8	3.2	8.4	43	33	1.3	

<sup>1</sup> Glenoid fossa geometric mean = (glenoid fossa height × glenoid fossa breadth)<sup>1/2</sup>.

<sup>2</sup> Proximal epiphysis geometric mean = (proximal epiphysis breadth × head vertical diameter × head transverse diameter)<sup>1/3</sup>.

<sup>3</sup> Proximal epiphysis geometric mean = (olecranon breadth × coronoid breadth × olecranon height × trochlear anterior-posterior diameter × coronoid height)<sup>1/5</sup>.

<sup>4</sup> Individual data from Maia Neto (1957).

Specimens of the Sima de los Huesos samples for:

Glenoid fossa geometric mean = AT-320, AT-343, AT-794, AT-1671 and Scapula I.

Humeral proximal epiphysis geometric mean = Humerus II, AT-25, AT-1103 and AT-1107.

Humeral midshaft perimeter = Humerus II, Humerus III, Humerus V, Humerus VI, AT-25, AT-93, AT-217, AT-658 and AT-1110.

Humeral biepicondylar breadth = Humerus II, Humerus III, Humerus VI, AT-790 and AT-1117.

Ulnar proximal epiphysis geometric mean = Ulna I, Ulna V, AT-488, AT-662, AT-1099, AT-1104 + AT-1105 (both belong to the same individual) and AT-1120.

Ulnar superior perimeter = Ulna I, Ulna V, AT-218, AT-488, AT-662, AT-1099, AT-1104 + AT-1105, AT-1120 and AT-1270.

Ulnar midshaft perimeter = Ulna I, Ulna II, Ulna V, AT-662, AT-883, AT-1104 + AT-1105, and AT-1270.

Radial neck perimeter = Radius I + AT-1109 (same individual), Radius II, Radius III, AT-1702 and AT-1147.

vidual was not fully adult (around 14 years old based on dental evidence), the cranial capacity would not have increased substantially in adulthood (Fig. 1).

It is interesting to note that Skull 5 and Cranium 4 almost span the whole European and African Middle Pleistocene range of cranial capacities (Table 2). Only Salé (Holloway, 1981) is substantially smaller than Skull 5, although there is a pathological abnormality in the occipital bone (Hublin, 1985) that could affect the cranial capacity of this individual. Omo Kibish 2 has a bigger cranial capacity than Cranium 4 (Day, 1986), but it can date to the late Middle Pleistocene or early Upper Pleistocene. In spite of this large range of SH compared to the rest of the Euro-African fossil record, the maximum ratio of the Sima de los Huesos sample is in the central part of the distribution of modern human random samples of three indi-

viduals (Table 6). The difference in the probabilities between Afro-American and Euro-American samples could be due to a more homogeneous composition of the former.

### Upper limb

In the Coimbra sample glenoid fossa dimensions show a relatively high sexual dimorphism, and the discriminant function performed for the maximum length and breadth of the glenoid cavity determined correctly the sex in 92.5% of the cases (n = 160) (Carretero, 1994). In the Coimbra distribution 43.9% of 1,000 modern samples display CVs greater than the Sima de los Huesos sample and in 31.0% of the samples the MR was above the SH value (Table 6).

Humeral epiphyses, and particularly the proximal one, are the most dimorphic regions of the humerus in modern humans (Dittrick and Suchey, 1986; Krogman and

TABLE 4. *Coxal and sacrum: Descriptive statistics (mm) for Coimbra pooled sex sample and Sima de los Huesos sample*

	Sample	n	Mean	SD	CV	Max.	Min.	MR	ISD
<b>Coxal</b>									
Vertical acetabular diameter	Coimbra	372	52.5	3.8	7.2	62	41.7	1.49	1.11
	SH	5	56.7	3.6	6.3	60.5	50	1.21	
<b>Sacrum</b>									
Lumbosacral surface geometric mean <sup>1</sup>	Coimbra	142	37.6	3.5	9.3	45.5	30.9	1.47	1.11
	SH	2	40.1	3.6	—	42.6	37.5	1.14	

<sup>1</sup> Lumbosacral surface geometric mean = (transverse diameter × anteriorposterior diameter)<sup>1/2</sup>.

Specimens of the Sima de los Huesos samples for:

Vertical acetabular diameter = AT-500, AT-800, AT-835, AT-1000 and AT-1004.

Lumbosacral surface geometric mean = AT-322 and AT-1003.

Işcan, 1986; Bass, 1987; France, 1988; Carretero, 1994; Carretero et al., 1995). In the SH humeral sample neither proximal epiphysis geometric mean variations nor biepicondylar breadth variations are unusual. In fact, the probability of finding modern samples of four individuals with MR above the SH value is 0.679 for the proximal epiphysis size and 0.694 for the biepicondylar breadth (Table 6).

Nevertheless, an unusual variation is found in the SH sample for the humeral midshaft perimeter (Fig. 2). In this case, only 25 of 1,000 samples (2.5%) yield MRs above that of the SH sample, although the proportion is somewhat higher for the CVs (12.5%) (Table 6).

Whichever the interpretation, it is surprising that neither the ulnar nor the radial shafts display the degree of variation found in the humeral shaft. The three ulnar regions we have explored (proximal epiphysis, proximal shaft and midshaft; Fig. 2) show a large CV in our modern human sample (Table 3) and the proportion of randomly generated samples with CV and MR larger than the SH sample ( $n = 7$  and  $9$ ) is very high for these three ulnar regions (Table 6). This is also the result for the radial neck perimeter (the only radial variable used). In this case the 58.4% and 46.0% of 1,000 random samples present CV and MR respectively above the SH sample values (Table 6).

#### Hip bone and sacrum

Sexual dimorphism of the hip bone in modern humans is well known (see Arsuaga, 1985a,b; Arsuaga and Carretero, 1994; Arsuaga et al., 1995a; and references therein). In particular, the acetabular size is highly dimorphic in modern humans (Fig. 3). In the

sample of known sex from Coimbra (Portugal) (Arsuaga, 1985a,b; Arsuaga and Carretero, 1994; Arsuaga et al., 1995a), a discriminant function for two acetabular diameters (vertical and transverse) determined the sex correctly in 83.8% of the cases ( $n = 398$ ).

In the Atapuerca SH sample, in five fossils with the Y-shaped suture of the hip joint fused (as well as the anterior inferior iliac spine), it is possible to take the vertical acetabular diameter (maximum acetabular diameter from the point where the axis of the ischial body intersects the acetabular rim). Two of them (AT-800 and AT-1000) show all epiphyses fused, one (AT-835) looks fully adult (or almost) although the regions of the iliac crest and ischial tuberosity are not preserved, AT-1004 shows the iliac crest non-fused and the ischial tuberosity fusing, and, finally, another fossil (Coxal I, the one with the smallest vertical acetabular diameter) shows the ischial tuberosity non-fused. In spite of the immature state of two of the fossils of the sample we consider that their acetabular diameters would not have increased because the Y-shaped suture is already fused (Fig. 4).

The coefficient of variation and the maximum ratio of the SH sample does not show an unusual value compared to the Coimbra distribution, 49.9% of the random samples yield CVs above that of the SH sample, and in 33.2% the MR was above that of the SH sample (Table 6).

The lumbosacral joint size is among the variables used by Jungers (1988) to estimate body size in australopithecines. In the SH sample only two specimens (AT-322 and AT-1003) are available for the study (Table 4). We have used these two specimens for the

TABLE 5. Lower limb: Descriptive statistics (mm) for the pooled sex comparison samples and Sima de los Huesos sample

Comparison sample		n	Mean	SD	CV	Max.	Min.	MR	ISD
<b>Femur</b>									
Head vertical diameter	Coimbra	146	43	3.4	7.8	50.5	34.1	1.48	1.12
	SH	4	45.6	4.1	—	52	42	1.24	
Midshaft perimeter	Coimbra	146	81.3	6.8	8.3	101	63	1.6	1.11
	SH	8	94.9	7.4	7.8	106	85	1.25	
Subtrochanteric geometric mean <sup>1</sup>	Coimbra	146	29.3	2.4	8.1	36.2	22.7	1.6	1.11
	SH	7	30.7	2.2	7.2	33.9	27.8	1.22	
<b>Patella</b>									
Patellar geometric mean <sup>2</sup>	Hamann-Todd Euro-Americans	50	31.8	2.7	8.6	37.1	24.8	1.5	1.13
	Hamann-Todd Afro-Americans	50	32.1	2.7	8.4	38.7	26.4	1.47	1.09
	SH	5	35.7	2.3	6.4	39.1	32.3	1.21	
<b>Tibia</b>									
Midshaft perimeter	Palencia	114	75.6	7.9	10.5	97	59	1.64	1.13
	SH	6	82.8	8.7	10.4	95	73	1.3	
<b>Talus</b>									
Trochlear geometric mean <sup>3</sup>	Palencia	106	29.2	2.3	7.9	35.3	24.4	1.44	1.11
	SH	8	29.9	2.1	7.1	33.4	27.3	1.22	
<b>Calcaneus</b>									
Geometric mean <sup>4</sup>	Coimbra	156	49.7	3.3	6.6	59.4	42.6	1.4	1.1
	SH	7	52.3	2.5	4.7	55.5	49.6	1.12	

<sup>1</sup> Subtrochanteric geometric mean = (subtrochanteric anteriorposterior diameter × subtrochanteric medio-lateral diameter)<sup>1/2</sup>.

<sup>2</sup> Patellar geometric mean = (maximum thickness × maximum height × maximum breadth)<sup>1/3</sup>.

<sup>3</sup> Trochlear geometric mean = (trochlear length × trochlear breadth)<sup>1/2</sup>.

<sup>4</sup> Calcaneus geometric mean = (maximum length × body length × sustentaculum breadth × body height)<sup>1/4</sup>.

Specimen of the Sima de los Huesos samples for:

Head vertical diameter = Femur IV + V (both belong to the same individual), Femur X, Femur XI and AT-1030.

Subtrochanteric geometric mean = Femur IV + V, Femur X, Femur XI, Femur XIII, AT-616, AT-1020 and AT-1030.

Femoral midshaft perimeter = Femur IV + V, Femur X, Femur XIII, AT-329, AT-432, AT-435, AT-616 and AT-999.

Patellar geometric mean = AT-338, AT-670, AT-1043 + AT-1044 (same individual), AT-1331 and AT-1783.

Tibial midshaft perimeter = AT-19, Tibia I, Tibia III + AT-848 (same individual), Tibia IV, Tibia V and Tibia VI.

Talar trochlear geometric mean = AT-860, AT-965, AT-966 + AT-980 (same individual), AT-1322, AT-1477, AT-1700, AT-1716 and AT-1822.

Calcaneus geometric mean = AT-489, AT-663, AT-967, AT-969, AT-971 + AT-981 (same individual), AT-1576 and AT-1740.

bootstrapping; Lockwood et al. (1996) have demonstrated that the results obtained with a bootstrapping of two elements are very similar to those using the exact randomization method (that compute all possible pairwise ratios). Again, size variation larger than between the two Sima de los Huesos sacra is found very often (30.4%) in the Coimbra distribution of 1,000 samples (Table 6).

### Lower limb

Because the loads borne by articular elements of the locomotor skeleton are closely linked biomechanically to body mass, measures of postcranial joint size should also be relatively reliable predictors of body size (McHenry, 1976; Jungers, 1988; Rightmire, 1986). Weight-bearing portions of the locomotor skeleton are arguably good candidates for being reliable estimators of overall body size (Jungers, 1988), and diaphyseal perim-

eters or circumferences (McHenry, 1976, 1988) and cross-sectional geometrical data (Ruff, 1990; Ruff et al., 1993) have been used for that purpose.

Femoral head diameters and proximal shaft widths are moderately correlated with body weights (McHenry, 1988; Ruff et al., 1991) but show marked sexual dimorphism in modern humans (Tamagnini and Saraiva, 1949; Genovés, 1962; Krogman and Işcan, 1986). Nevertheless, among the 1,000 modern samples generated randomly, for the head vertical diameter and proximal (subtrochanteric) and middle shaft perimeters the CVs and MRs are larger than in the SH sample (Table 6, Fig. 4).

It is not yet possible to study the distal femur directly, but the patella (n = 5) could be a rough approximation of the knee size variation in the SH sample (Fig. 5). The size variation found in SH patellar sample does



TABLE 6. Percentage of samples generated randomly ( $n = 1,000$ ) above *Sima de los Huesos* coefficient of variation (CV) and maximum ratio (MR)

		SH	Coimbra		Palencia		Hamann-Todd Euro-Americans		Hamann-Todd Afro-Americans	
		n	CV	MR	CV	MR	CV	MR	CV	MR
Cranium	Cranial capacity	3	—	—	—	—	—	44.7	—	25
Scapula	Glenoid fossa geometric mean	5	43.9	31	—	—	—	—	—	—
Humerus	Proximal epiphysis geometric mean	4	—	67.9	—	—	—	—	—	—
	Midshaft perimeter	9	12.5	2.5	—	—	—	—	—	—
	Biépicondylar breadth	4	—	69.4	—	—	—	—	—	—
Ulna	Proximal epiphysis geometric mean	7	—	—	90	90.3	—	—	—	—
	Proximal perimeter	9	—	—	88.8	77.5	—	—	—	—
	Midshaft perimeter	7	—	—	67.1	68.5	—	—	—	—
Radius	Neck perimeter	5	58.4	46	—	—	—	—	—	—
Coxal	Vertical acetabular diameter	5	46	31.4	—	—	—	—	—	—
Sacrum	Lumbosacral surface geometric mean	2	—	30.4	—	—	—	—	—	—
Femur	Head vertical diameter	4	—	18.4	—	—	—	—	—	—
	Subtrochanteric geometric mean	8	36.7	56	—	—	—	—	—	—
	Midshaft perimeter	7	33.6	50.9	—	—	—	—	—	—
Patella	Geometric mean	5	—	—	—	—	68.2	64.7	64.5	56
Tibia	Midshaft perimeter	6	—	—	30.2	42.3	—	—	—	—
Talus	Trochlear geometric mean	8	—	—	50.7	61	—	—	—	—
Calcaneus	Geometric mean	7	77.4	90.9	—	—	—	—	—	—

not exceed the normal variation found in both Hamann-Todd subsamples (Table 6). The same is the case for the tibial midshaft perimeter. In this case, 30.2% and 42.3% of 1,000 samples of six individuals display CVs and MRs, respectively, larger than the SH values (Table 6).

The talus and calcaneus have a critical participation in the transmission of the weight to the rest of the foot and to the ground and in the energy absorption during walking. Thus the size and articular surfaces of these two bones should be correlated with body weight. For the talus we have calculated the geometric mean of the two trochlear basic dimensions, length and breadth. In the Palencia sample distribution of 1,000 samples of eight individuals, 50.7% and 61% of them display CVs and MRs, respectively, greater than in the SH sample (Table 6, Fig. 5). In the case of the calcaneus we use as expression of size the geometric mean of four variables (Table 5). Fully 77.4% of 1,000 samples have CVs above that of the *Sima de los Huesos* sample and 90.9% of them have MRs above the *Sima de los Huesos* value (Table 6, Fig. 5).

We should note that within samples, shaft variation (CV and MR) in lower limb bones (femur and tibia midshaft perimeters) and

foot bones size variation (talus and calcaneus) are lesser than in the upper limb bones (humerus, radius and ulna midshaft perimeters) (Table 3 and Table 5). In other recent human samples Trinkaus et al. (1994) also found a consistent pattern in which lower limb shaft asymmetry values are lesser than in the upper limb.

## DISCUSSION AND CONCLUSIONS

Bermúdez de Castro et al. (1993), who analyzed only the lower dentition, concluded that sexual dimorphism in teeth was more marked in the *Sima de los Huesos* sample than in modern humans, contrary to the conclusions stated by Arsuaga et al. (1997a). The former authors also observed that the Krapina Neandertals (dated to c. 130 kyrs by Rink et al., 1995) showed a decrease in the magnitude of dental sexual dimorphism with respect to the SH fossils, but that the Krapina dental sample was still more dimorphic than are modern humans. Nevertheless, there exists no biomechanical reason to expect a direct or especially predictable relationship in humans between skull or teeth variables and body size. In fact, Bermúdez de Castro and Nicolás (1995) found that the correlation coefficients between femur length and crown area of the molars in the Coimbra

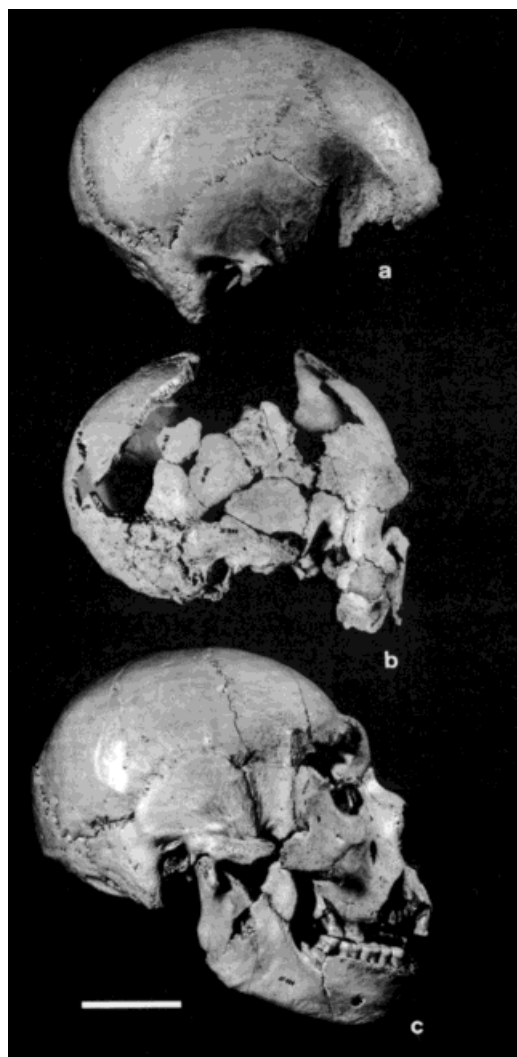


Fig. 1. Three crania from the Sima de los Huesos site. Cranium 4 (a), the largest specimen with 1,390 cm<sup>3</sup> of cranial capacity, Skull 6 (b) with 1,220 cm<sup>3</sup> of cranial capacity and Skull 5 (c), the smallest specimen with 1.125 cm<sup>3</sup> of cranial capacity. The scale bar represents 5 cm.

sample ( $n = 155$ ) range from 0.02 to 0.35. Garn et al. (1967) reported low correlations between mesiodistal and buccolingual dimensions of all the teeth and stature in a sample of Caucasoids. Henderson and Corruccini (1976) also found low correlations between canine size and body size in a sample of Afro-Americans. All these authors concluded that dental size to body size inferences in hominids are unwarranted. Finally,



Fig. 2. The largest and the smallest specimens in the Sima de los Huesos sample for the scapular glenoid fossa (a = AT-794; b = AT-1671); humeral shaft (c = AT-93; d = AT-1110); humeral distal epiphysis (e = AT-1110; f = AT-1105; g = AT-662). The scale bar represents 2 cm.

Frayer and Wolpoff (1985) have also suggested that tooth sexual dimorphism and body sexual dimorphism may not go hand in hand during human evolution.

In the Sima de los Huesos collection, the postcranial skeleton does not show an unusual size variation compared to the distribution of samples of the same size randomly generated from sex-balanced modern human samples. Only the humeral midshaft perimeter shows an extreme maximum ratio in the Sima de los Huesos group, though a less exaggerated coefficient of variation (Table 6).

The size variation found in the SH humeral shaft dimensions could be interpreted as age related. The specimen with the biggest midshaft perimeter, AT-93, is an adult (Fig. 2 and for discussion see Carretero et al., 1997). The smallest specimen, AT-1110, a distal half with the epiphysis completely

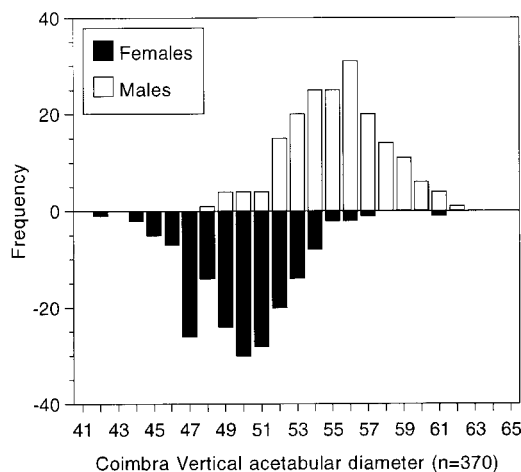


Fig. 3. Frequency histograms of the vertical acetabular diameter of the Coimbra modern human sample ( $n = 370$ ).

fused (Fig. 2), is older than 16–18 years. Yet, although no trace of immaturity is appreciated in the external aspect of AT-1110 and we believe it is adult, theoretically it could be not fully adult since in modern humans the humeral proximal epiphysis unites with the diaphysis somewhat later (at 19–20 years) than the distal one. Nevertheless, if it were only 18–19 years old the humeral dimensions would not have increased substantially with age.

A second possibility to explain this shaft variation is arm side (behavioral) dominance. However, both extremes of variation in the SH sample come from the right side. It could still happen that the smallest specimen (AT-1110) would correspond to a left-handed individual, and the largest humerus (AT-93) to a right-handed individual. Handedness has characterized the SH hominids (Bermúdez de Castro et al., 1988) and most Pleistocene members of the genus *Homo* (Falk, 1980; Holloway, 1981; Holloway and De La Coste-Lareymondie, 1982; Toth, 1985; Trinkaus et al., 1994). According to Bermúdez de Castro et al. (1988), all the SH hominids were right-handed so it is highly likely that both AT-1110 and AT-93 would correspond to right-handed individuals and we can reasonably exclude laterality as an explanation for the differences in midshaft perimeter between AT-1110 and AT-93.



Fig. 4. The largest and the smallest specimens in the Sima de los Huesos sample for the acetabulum (a = AT-1000; b = Coxal I) and the proximal femur (c = Femur X; d = Femur XI). The scale bar represents 2 cm.

The large humeral midshaft perimeter variation found in SH could have an important environmental component, since bone sections and circumferences have been associated with habitual behavioral patterns, as shown by the asymmetries due to functional lateralization found in extant human populations and in fossil samples (Borgognini-Tarli and Repetto, 1986). Recent humans show relatively little bilateral asymmetry in humeral length or distal articular breadth, but larger and more variable asymmetry in diaphyseal cross-sectional geometric parameters (Trinkaus et al., 1994). Diaphyseal cross-sectional geometry variables (medullar area, cortical area and second moments of area) are highly correlated with the shaft external dimensions and small variations in midshaft diameters and/or perimeters result in high increments of those cross-

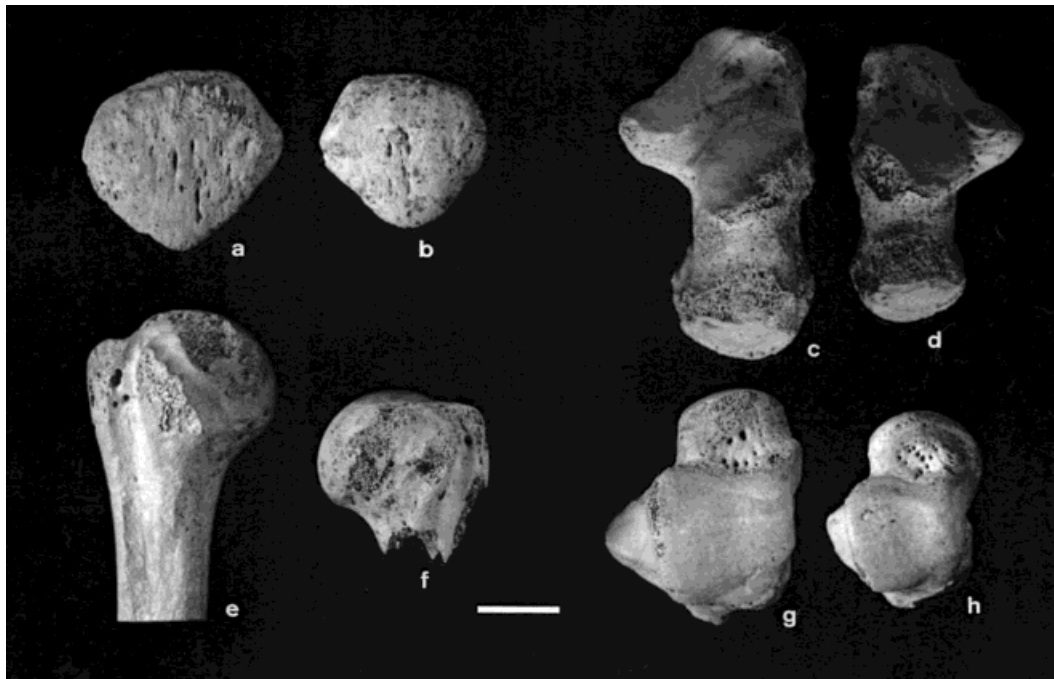


Fig. 5. The largest and the smallest specimens in the Sima de los Huesos sample for the patella (a = AT-1783; b = AT-1331); calcaneus (c = AT-969; d = AT-663), humeral proximal epiphysis (e = AT-25; f = AT-1103) and talus (g = AT-1165; h = AT-1716). The scale bar represents 2 cm.

sectional geometry variables. Trinkaus et al. (1994) conclude that "a major component of the changes in humeral diaphyseal robusticity apparent through the genus *Homo* is load (hence activity) related." Unfortunately, no attempt was made by Trinkaus et al. (1994) to compare directly the asymmetry values in external midshaft diameters and perimeter, and thus their results are not directly applicable to the understanding of the high variation of the SH midshaft perimeter. On the other hand, in a study of the Coimbra population, Themido (1926) found very low asymmetry values for shaft diameters and minimum perimeter (around 2.5% in males and 1.1% in females, calculated on the right and left averages). If the large humeral midshaft differences found in the SH sample are related to muscular activity variation, an extraordinary amount of it should be assumed (related or not with sexual division of labour within the group).

Regarding cranial capacity, the variation observed in the Sima de los Huesos sample is not at all atypical for modern humans,

even though the SH range (of a sample of only three specimens) almost embraces the whole European and African Middle Pleistocene range of cranial capacities.

Consequently, the widely accepted cliché that sexual dimorphism has experienced a dramatic decrease in modern populations (De Lumley and De Lumley, 1974; Wolpoff, 1980; Frayer and Wolpoff, 1985) and that the sexual dimorphism of the Middle Pleistocene hominids is higher than in modern humans is not supported by the Sima de los Huesos cranial and postcranial evidence.

In our opinion, analyses of sexual dimorphism in Middle Pleistocene or Neandertal samples (or other Prehistoric samples) may be confounded by the a priori sexing of the individuals (which may overestimate dimorphism), and especially by the large geographic and chronologic ranges covered by the fossil samples. Both factors add substantial variation due to interpopulational differentiation or to phyletic evolution (either directional or fluctuating). In fact, if the degree of sexual dimorphism were not much



greater than in modern human populations, the latter two sources of variation might contribute more to the variation of the fossil sample (even separately) than sexual dimorphism. When a sample deriving from a single contemporaneous population is used, as the Sima de los Huesos sample, and its variation is compared to the intrapopulation variation in modern humans, a more marked cranial and body sexual dimorphism in the Middle Pleistocene sample is not apparent.

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